The Evolution of Coorperation and Game Theory

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Abstract

Lower lifeforms such as bacteria and viruses sometimes exhibit some form of social interaction. It has been shown that some "creatures" such as the $\phi 6$ virus and the bacterium Escherichia coli tend to act in a social context to give their neighbors a benefit while simultaneously they do not have an advantage of this. This behavior is called cooperation and in human beings its some kind of cognitive behavior. Because unicellular and even viruses lack the cognitive ability to interact, it has to be explained by other mechanisms. Mathematical game theory is often used because this model fits best. How cooperation in these life forms and higher lifeforms has been evolved is a topic of high interest and the possible roots of this behavior will be discussed in this review.

Introduction

Evolution is a filtering mechanism which tends to keep the fittest and remove the other ones. In a biological context, it describes the way of a life-form which evolves more and more to a better or fitter life-form as time goes on. Each individual tries to promote its own evolutionary success even when this means it has to steal someones else resources, resulting in a disadvantage for the other individual. However in contrast to the survival of the fittest strategy of an individual, evolution has also promoted the strategy of cooperation which has led to higher lifeforms. This means there also exist groups which act together like genes in genomes or on a higher level cells in multicellular systems. Furthermore there are groups of individuals from the same species which cooperate with each other to have an advantage over other individuals of other species which leads to a fitter population. Without cooperation the world would only contain individuals on a micromolecular level.
Cooperation has to be differently interpreted depending on the individual considered. In higher lifeforms like mammalians individuals cooperate with each other if they get any kind of advantage. In this case, cooperation is the result of cognitive behavior. In lower lifeforms, lack of a brain or something comparable like a neuronal network e.g. a ganglion, cooperation is just a term to describe the behavior of individuals of a closed system. If an organism produces a good for its own and some other organism steals this good then the producer cooperates with the thief or defector although this was not the intention of the "cooperator".

The remainder of this review is organized as follows. First of all a few definitions on the terms used are given. After that five different types of cooperation mechanisms [?] will be described and a rule is derived if one individual or group cooperates with another one or not. At last an example of cooperation in the sense of cheating viruses [?] is given.

Preliminaries

To describe and distinct cooperation and selfish behavior it is necessary to define what cooperation means in detail especially in this review and what a cooperator and a defector is. Cooperation, in this context, is defined as an interaction between a donor (cooperator) who pays a cost c so that some other individual gets a benefit b. This is also known as altruism because the donor is acting selfless for the welfare of others. A defector never pays a cost but is able to receive benefits as cooperators do. This definition is expanded by requiring that the benefit of the receiver has to be bigger than the costs for the donor, ensuring that the mathematical definitions for evolution of cooperation are valid. This leads to a simple mathematical formula which states that the benefit to costs ratio is greater than one.

$$\frac{benefit}{cost} > 1 \tag{1}$$

From that simple but efficient equation and the definitions for cooperators and defectors given above a general mathematical model has been derived to describe the interactions between the different individuals. The presented model measures the costs and benefits in terms of fitness of the individual respectively the population. This leads to the question, how fitness can be measured. In this review fitness will be defined as the capability to reproduce in a specific amount of time. Thus, the faster an individual reproduces the bigger the fitness. An overview about the costs and benefits when cooperators and defectors interact with each other is given in equation 2 as a payoff matrix. Here C stands for a cooperator and D for a defector. The matrix is read from left to right which means it refers only to the row player.

$$\begin{array}{cc} & \begin{array}{cc} \text{C} & \text{D} \end{array} \\ \begin{array}{c} C \\ D \end{array} & \begin{pmatrix} b-c & -c \\ b & 0 \end{pmatrix} \end{array} \tag{2}$$

Four cases can be distinguished. If a cooperator C interacts with another individual then a cost c is payed. Interaction with a cooperator on the other side leads to a benefit b. From the given payoffs the matrix has been derived. It can be seen that an interaction between two defectors leads to a payoff of zero. In contrast cooperation between two cooperators leads to payoff $b-c$. If the payoffs of the two interactions are compared a constraint has to be fulfilled otherwise cooperation would be non sensical. This constraint is the one which is stated in equation 1. The benefit has to be bigger than the costs. In terms of fitness costs and benefits it can be seen in the following way. Suppose there are two individuals which interact with each other. The first individual sacrifices on his offspring (costs) so that the other one is able to produce more offspring as he would usually do (benefit) when the first individual would produce his offspring too.

So given the fact that the defectors are able to increase their fitness and never decrease it while cooperators do, a simple statement can be formulated. In a mixed population of cooperators and defectors, defectors have a bigger net benefit than cooperators when interacting with a cooperator. Because benefit is a measure of fitness the defectors fitness increases faster then the fitness of the cooperators. This means they evolve faster than the cooperators and at the end cooperators will vanish because of their fitness deficit. This is schematically shown in figure 1 where after an amount of time the cooperators were erased.

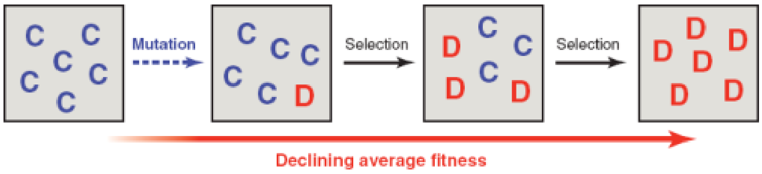

Figure 1: The evolvement of defectors and the reduction of cooperators, when only the survival of the fittest strategy holds and no mechanism for the evolution of cooperation exist.
[Source: Nowak,M A. 2006. Five rules for the evolution of cooperation. Science,Vol.314.]

Because of this the question arises why cooperation exists and the answer will be given in the next part.

Types of Cooperation

The reasons why natural selection sometimes favors the evolution of cooperation is divided in five parts which will be discussed in the following. It will be shown that the mechanisms are different from each other, but in the end all of them can be described by a simple mathematical rule.

Kin Selection

Kin selection is the first mechanism described here why cooperation evolves. The idea behind this mechanism is that individuals which are related by some feature tend to cooperate when the degree of relatedness is bigger than the cost to benefit ratio. To show how this works in detail consider the situation which is shown in figure 2. There are two siblings which share $\frac{1}{2}$ of their genetic content so the degree of relatedness is here $r = \frac{1}{2}$. Each offspring of the two siblings would have $\frac{1}{4}$ of the genetic content of the grandparents. If A and B both produce two offspring the net amount of the genetic content of the grandparents would be 1. But if A sacrifices on his offspring and B produces seven then the net amount is $\frac{7}{4}$ which is clearly bigger then 1 and bigger than the relatedness of $\frac{1}{2}$ between the siblings.
This behavior was first described by the mathematician Hamilton in 1964. He formulated on the situation described above a simple formula which is widely known as Hamilton's rule.

$$r > \frac{c}{b} \tag{3}$$

It states that one individual cooperates with another if and only if the two individuals are related to each other and the coefficient of relatedness r exceeds

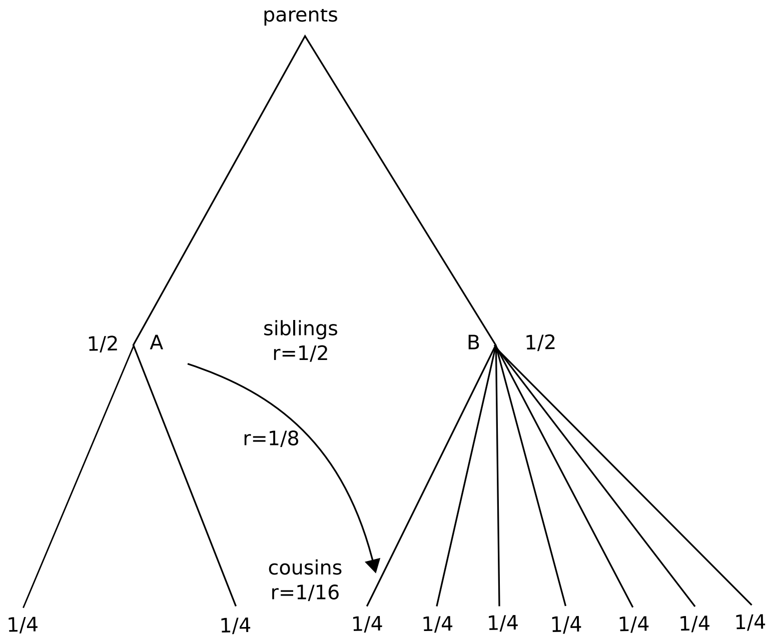

Figure 2: An example for kin selection based on genetic relatedness. If A sacrifices 2 of his offspring and subsequently B is able to have 7 offspring instead of only 2 when A would have not sacrificed his offspring. By applying Hamilton's rule to this case it becomes clear that selection favors cooperation.

the ratio between costs c and benefit b. The coefficient of relatedness in the example above was defined by the probability of sharing a common gene, e.g. $r = \frac{1}{2}$ when individual A and individual B are siblings. Here it is implicitly given that the benefit b has to be greater the costs c a cooperator has to pay otherwise the probability r would not be defined. The kind of relatedness can be defined as arbitrarily as necessary.

Direct Reciprocity

Another more general mechanism for the evolution of cooperation is the principle of direct reciprocity. It is based on the idea that if individual A gets a benefit from individual B then individual A will be thankful and probably will give B a benefit too. This kind of direct reciprocity is visualized in figure 3.

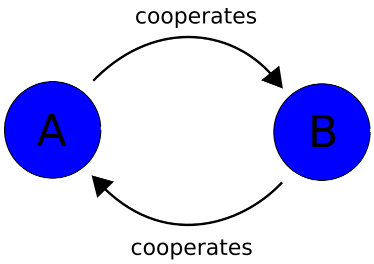

Figure 3: Principle of direct reciprocity. If A cooperates with B than B will probably cooperate with A too.

This is a simple but effective mechanism of cooperation. It is more general than kin selection because it does not matter if the two cooperating individuals are related to each other or not. The only requirement is that someone must be the first to cooperate. In nature, this is realized if one individual in a group of defectors has a mutation and becomes a cooperator. When the cooperator now meets another individual and gives him some benefit, this individual will probably cooperate as well.
Based on this mechanism someone can now simulate what happens with a population where cooperation is present. This is the point, where mathematical game theory is the model of choice to explain the evolution of cooperation. It assumes that in each round two players interact with each other. A player has the choice between cooperation and defection. His decision to cooperate or to defect is based on a function which maximizes the players payoff. This kind of game is also known as the prisoner's dilemma. For direct reciprocity there exists a variant of this game which is called iterated prisoner's dilemma. Here player B who has gotten a benefit or not from player A in the previous round now decides to cooperate with player A or not. A player wins when he reaches a specific amount of benefit. Now it is interesting to know which strategy someone should follow to win the game. The simplest one is called tit-for-tat and means that the first player starts in the first round with a cooperation and then he does whatever the second player has done before. A second more sophisticated strategy is called generous tit-for-tat. It is based on the same principle as the simple tit-for-tat except that with a probability of $1 - \frac{c}{b}$ the first player cooperates again although the second player defected in the previous round. There are a lot of other strategy known for this type of game.
To come back from game theory to the mechanism for the evolution of cooperation a simple mathematical rule can be derived as it was possible for kin selection. The mechanism of direct reciprocity is favored by natural selection if the probability w of two individuals to meet each other again exceeds the cost to benefit ratio which is shown in equation 3.

$$w > \frac{c}{b} \tag{4}$$

Indirect Reciprocity

The third mechanism which can lead to the evolution of cooperation just refers to higher lifeforms like mammalians and especially humans because some cognitive capabilities like speech and memory are necessary. In contrast to direct reciprocity it is not necessary that two individuals meet twice. This type of cooperation is based on a slightly different mechanism. Here the decision of cooperation with a recipient is based on the knowledge about his reputation. It is possible to lower and to upper the reputation based on the individuals behavior. If an individual cooperates often then it will increase its reputation. If someone never or barely cooperates then this will lower its reputation.

It is intuitive that individuals with a good image will receive benefits more often from cooperators than those with a bad image. The decisive criteria for someone is his knowledge about the reputation of his interaction partner.

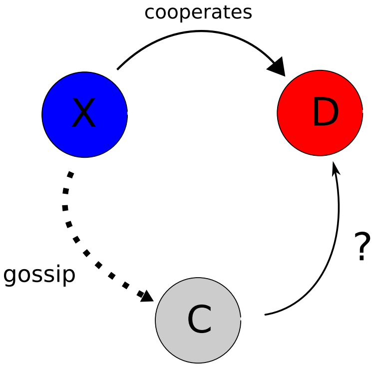

Figure 4: Principle of indirect reciprocity. If X cooperates often with B and tells this a third individual C then C will base his decision to cooperate with B on his knowledge about B's reputation.

To visualize these statements an example is given in figure 4. If individual X cooperates often with B and B never cooperates then B will decrease his reputation and A will increase it. Furthermore A knows now B's reputation and tells individual C about it. If C now meets individual B he will base his decision for cooperation with B on his knowledge about B's reputation. To describe this behavior mathematically one can consider the following payoff matrix.

	C	D
C	$b-c$	$-c(1-q)$
D	$b(1-q)$	0

If cooperator C in the first row meets a defector D in the second column then he will only cooperate and pay a cost c if he does not know the reputation of D which is equivalent of $q = 0$, the probability to know someones reputation. As opposed to this if C knows the reputation of D then the probability q to know someones reputation is 1 and C will not pay any costs. Symmetrically in the lower left corner can be seen what this means for the benefit of a defector. He will only get the full benefit from a cooperator if this one does not know the reputation of the defector.
To summarize all this considerations another formula has been stated. It states that if the probability q to know someones reputation is bigger than the cost to benefit ratio someone will cooperate as can be seen from equation 5.

$$q > \frac{c}{b} \tag{5}$$

Network Reciprocity

This fourth approach seems to be more realistic than the previous three ones because it also models spatial separation.
It is modeled by an interaction graph where the nodes are cooperators or defectors and edges indicate the possibility of interaction. This means that a node can only interact with another node if they are connected. This is the spatial component of this model, because it is possible to separate groups from each other by removing the edges between them. Caused on the connection property a node who cooperates automatically deals out benefits for all of his neighbors. This means a node who has a lot of neighbors will more often receive benefits than a node with only a few neighbors. The fitness of a node is described by equation 6.

$$F = 1 - \omega + \omega c \tag{6}$$

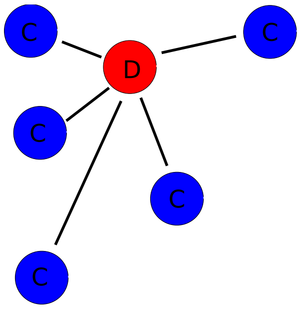

Figure 5: The defector has 5 neighbors which means his selection frequency ω is relatively high compared to the five cooperators. Because he never pays a cost c his overall fitness is drastically decreased by the amount of the selection frequency ω.

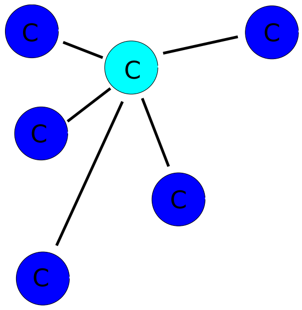

Figure 6: Here the cooperator has also 5 neighbors but sometimes he also deals out benefits and pays some cost. Because of that he is able to increase his fitness by the product of costs and selection frequency.

This formula discriminates between defectors and cooperators and can be easily understand. In the beginning each individual has a fitness of 1. Depending on the number of neighbors k, it has a big or small selection frequency ω. The individual's fitness will be reduced according to the selection frequency. At this point cooperators and defectors would have the same fitness. So another term is added to the fitness of cooperators to reward the dealing out of benefits. And this term is just the product of his selection frequency ω and the costs c he pays for cooperation. Considering figures 5 and 6 and putting the values for ω into formula 6, it can easily be seen that the fitness for the cooperator is bigger than that of the defector.
The last question to answer is, when does natural selection favors network reciprocity as a type of cooperation. If the benefit to cost ratio exceeds the average number of neighbors k natural selection favors cooperation as can be concluded from equation 7.

$$\frac{b}{c} > k \tag{7}$$

Group Selection

The last mechanism for the evolution of cooperation is called group selection. Here lies the main aspect on groups of individuals albeit the individual's behavior influences whether the groups fitness increases or decreases. It is easy to imagine that a group of pure cooperators growths faster than a group of pure defectors because cooperators in contrast to defectors deal out benefits in terms of fitness.
A group splits into two if it reaches a specific size so that cooperator groups are the fittest when viewing only on pure groups of cooperators and defectors. More interesting is what happens with mixed groups containing cooperators

and defectors. When looking at the individuals in this group it is clear that defectors reproduce faster than cooperators because they do not pay a cost and receive benefits for free. In this group it can be observed that the fitness of the defectors increases and the fitness of the cooperators decreases so that a specific amount of time cooperators will vanish as it has been visualized in figure 1. But because a pure group of defectors has a lower fitness than a pure group of cooperators the defectors group will vanish after some time. Because of that there has to be some kind of equilibrium between the number and reproduction rate of defectors and cooperators in a mixed group so that this group will not be vanished when time goes on. The two main observations from the facts given above are that selection within groups favors defectors and that selection between groups favors cooperators.
The derived rule given in formula 8 tries to describe a way why cooperation takes place.

$$b/c > 1 + (n/m) \tag{8}$$

It states that if the benefit to cost ratio is bigger than 1 plus the additive quotient of group size n and the number of groups m cooperation can evolve.

Cheating viruses

The most interesting thing is that viruses which often act as parasites in human bodies can also be parasites for other viruses if they coinfect an already infected cell. The subsequent events can be described with the same definitions which had been used in the first part of this review. Some viruses function as cooperators while others act as defectors. Nevertheless it is not the same kind of cooperation as described above because in the current context the cooperators were unvoluntary victims of their own inherently behavior, which is to be a parasite.

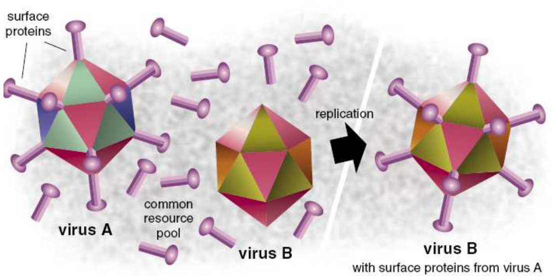

Figure 7: An example of cheating viruses. Virus B acquires the proteins of virus A and evolves to a new virus with foreign surface proteins.

[Source: Turner,P E. 2005. Cheating Viruses and Game Theory. American Scientist,Vol.93.]

When a virus enters a cell it hijacks the hosts metabolism to produce his own viral proteins. If now a second virus of different nature enters the same cell this one is able to hijack the host cells metabolism too and also produces his own viral proteins. As it can be seen in figure 7 both viruses are now able to use the other ones viral proteins because they are freely available in the cell body. This type of behavior is called complementation and in the case of figure 7 it is more precisely called phenotypic mixing because here a virus acquires phenotypic traits of another one. An example for this in nature are crop infecting umbraviruses which steal some of the capsid proteins of luteoviruses when both infected the same cell. Because of the new acquired proteins umbraviruses are now able to attach to aphids so that they can now spread more easily and infect more plants than the umbraviruses without this capsid proteins.

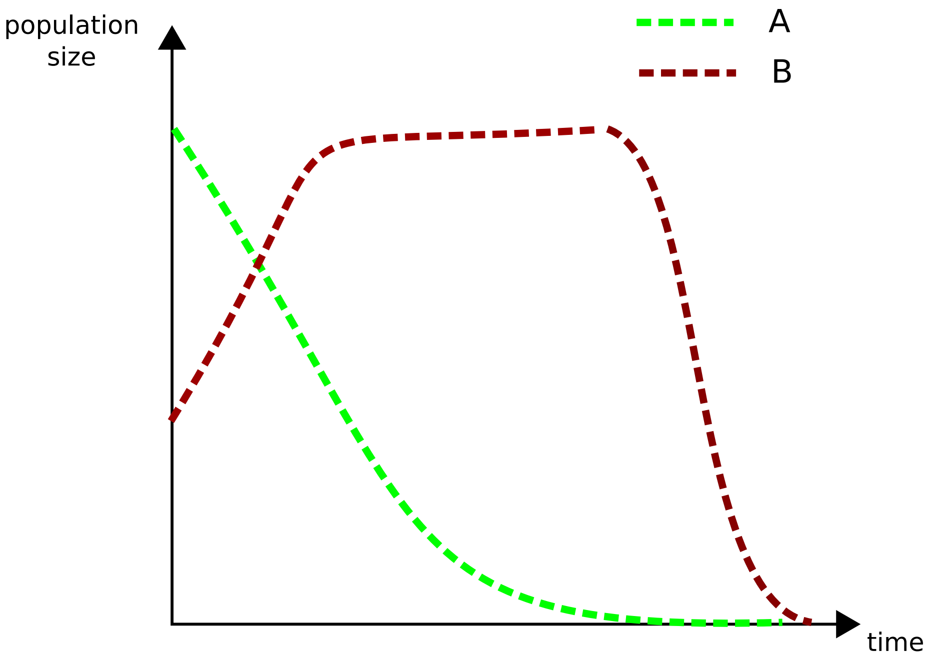

Figure 8: Plot of the population dynamics when viruses act as parasites on other viruses. In the beginning B has a big advantage of stealing A's resources. But because of that A becomes distinct and B will vanish too because at some point B has lost his ability to survive without any other help.

The evolutionary advantage here is immense, but it can also happen that this advantage in the beginning becomes a huge disadvantage. Suppose the case of two viral populations A and B which live at the same location and compete for the same resources and both produce a replication enzyme to replicate themselves. Now population B recognizes that the replication enzyme of population A is suitable to reproduce themselves. What now takes place is called section pressure, but can also be interpreted as cooperation. Population B now "decides" to lose the genes for his own replication enzymes and shortens its genome because population A produces enough enzymes for both in the beginning. Because of the shortened genome population B is able to reproduce faster than population A. This means its size increases drastically in relation to the size of population A. Because B gets bigger and bigger and steals more and more replication enzymes from A the members of A have less and less replication enzymes for themselves which is shown in figure 8.
At some time A will be extinct, because of his inability to reproduce caused on the continuous thievery of his own enzymes by B. As a direct consequence B will die out too because it lost its genes for his replication enzymes and A's replication enzymes were not longer produced. This is a negative example when evolution favors cooperation but leads in the end to extinction of cooperators and defectors which shows that evolution is not always advantageous.

Discussion

The five rules for the evolution of cooperation handle only cases where the benefit to cost ratio is bigger than 1. But especially when looking on kin selection where the degree of relatedness is the decisive factor for cooperation a crucial point has not been considered. Humans especially relatives sometimes cooperate although if they pay more as the receivers get. The mathematical formulas cannot handle this case, because it is not defined in the context from which the formulas were derived. On the other hand the formulas are quite simple and effective. Someone could also treat the special case mentioned above but this would probably lead to more complicated formulas and someone has to think about all the factors which has to be included.

Conclusion

The first part shows that the roots for the evolution of cooperation are of different nature, but have one thing in common. All of them can be described by a simple mathematical formula which follows only one principle namely that the benefit has to be bigger than the costs plus an additive term depending on the used model. The second part has shown that cooperation is also present in viruses which are most of the time not described as lifeforms. At the end it should be clear that cooperation leads to lifeforms with increased fitness compared to non cooperating individuals so that cooperation drives the evolution of individuals forward.

References